

Spatial and temporal patterns of abundance and the effects of disturbance on under-boulder chitons

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Abstract

The spatial and temporal patterns of abundance of 8 species of chiton found under boulders were documented at sites in the mid- and low-shore regions of an extensive boulder-field in the Long Reef Aquatic Reserve. The mean number of species and mean densities of *Ischnochiton australis* (Sowerby, 1840), *Ischnochiton elongatus* (Blainville, 1825), *Ischnochiton versicolor* (Sowerby, 1840), *Cryptoplax mystica* (Iredale & Hull, 1925), *Callistochiton antiquus* (Reeve, 1847), *Ischnochiton smaragdinus* (Angus, 1894) and *Acanthochiton* spp. did not vary through time during the 6 month study, conducted over the autumn and winter months. However, their abundances varied at small (areas 3 m apart) and large (sites 60 m apart) spatial scales in the mid- and low-shore regions. Abundances ranged between 0 and 28 individuals 1000 cm² of boulder surface over the study period.

Relationships between the abundances, sizes and numbers of species and the size of the boulder and/or the underlying sediments were rare, contrasting with suggestions made in early taxonomic studies. However, the sizes of *I. australis* in the low-shore and *I. elongatus* in the mid-shore were positively correlated with boulder size and the density of *I. elongatus* was positively correlated with the proportion of fine grained sediment.

A manipulative field experiment was done to examine possible sampling-induced changes in abundances. The mean number of species, total number of individuals and mean densities of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor* all declined following the overturning of boulders. The experiment also showed that despite the alterations to the habitat caused by our sampling, the abundances of the under-boulder chitons were not significantly altered. Therefore our data documenting patterns of abundance in space and time were not confounded by sampling-induced disturbance.

Introduction

Chitons have a worldwide distribution and are particularly abundant and speciose on the west coasts of North and South America and in Australasia (Dall 1919, Iredale and Hull 1927, Otaiza and Santelices 1985). Recent studies (e.g. Paine 1984, Duggins and Dethier 1985) have suggested that chitons play a major role in structuring the low-shore algal communities on rocky shores. In contrast,

little, if anything, is known about the ecology of chitons inhabiting boulder communities. The information that is available is restricted to about 20 species and concerns their taxonomy (Smith 1960), abundances and diets (Andrus and Legard 1975, Fulton 1975) and reproduction (Creese 1986). Chitons are often the most prevalent of the molluscan grazers found under boulders (Morton and Miller 1968, McGuinness 1984). It is not known at this stage whether they have any demonstrable effects on the other organisms comprising this community. In addition to possible effects on the abundances of algae, chitons could affect the densities of sessile organisms through the "bulldozing" (*sensu* Dayton 1971) and/or inadvertent consumption of new recruits.

Boulder communities are useful sites in which to study the development and maintenance of marine benthic communities. Research in these habitats (*e.g.* Osman 1977, Leiberman *et al.* 1979, Sousa 1979, McGuinness 1987a, b) has examined concepts of community stability, species-area relationships, successional changes and the effects of physical disturbance on community structure. A diverse group of organisms including ephemeral and perennial algae (Sousa 1979, Leiberman *et al.* 1979), and sessile (*e.g.* barnacles, tubeworms, sponges and ascidians) and mobile (*e.g.* polychaetes, limpets,periwinkles and chitons) animals (Pope 1943, McGuinness 1987a, b) make up these communities. Boulder communities are also important habitats for the recruitment of sea urchins (Tegner and Dayton 1977, 1981) and abalone (Shepherd 1973, Sainsbury 1982), animals that are important as marine herbivores and as seafood.

The ecology of chitons in Australia is poorly studied. Apart from taxonomic studies (*e.g.* Allan 1950, MacPherson and Gabriel 1962), there are a few studies which deal with aspects of reproduction (Turner 1978, Sakker 1986, Wells and Sellers 1987) and only a handful of studies on the distribution and abundance, diets, movement and effects of grazing (Thorne 1967, Otway 1989, 1994). This situation is made worse when one considers that a large proportion of Australian chitons are found under boulders and that the present ecological information concerning this habitat is restricted to three studies, those of Pope (1943), Kangas and Shepherd (1984) and Currie (1990). Consequently, much of the information concerning the distribution and abundance of under-boulder chitons in Australia must be inferred from the descriptive and taxonomic accounts (Pope 1943, Allan 1950, MacPherson and Gabriel 1962, Dakin 1952). These suggest that distribution and abundance are influenced by factors such as boulder size, sediment type and height on the shore.

Given the paucity of information concerning under-boulder chitons in SE Australia, our study was designed to examine three principal areas of interest. First, we considered it important to test the prior assertions of Dakin (1952) who inferred relationships between the distribution and abundance of under-boulder chitons and boulder size, sediment type and height on the shore. Second, we documented the spatial and temporal patterns of abundance of under-boulder chitons. Third, we used a manipulative field experiment to examine the effects of sampling-induced disturbance on the abundances of under-boulder chitons.

Materials and methods

This study was done at Long Reef Aquatic Reserve, Collaroy, N.S.W. (33°45'S, 151°19'E). The headland of Long Reef is surrounded by an extensive rock platform interspersed with small, sandy beaches and boulder zones. The platform, boulders and surrounding cliff faces consist of Collaroy Claystone ("chocolate shale") of the Narrabeen Group (McElroy, 1969). The study was done in the boulder field adjacent to Collaroy Beach, on the northern side of the headland, and is partially protected from the dominant south-easterly swell. Sampling was done during low water and boulders were collected from areas located 0.0 to 0.5 m above Mean Low Water Springs (chart datum for Sydney). The under-boulder community here is similar to that of other boulder fields along the N.S.W. coast (Dakin 1952, McGuinness 1987a, b).

Boulder Size

The surface area of the underside of each boulder was estimated by measuring appropriate

dimensions of the boulder. For example, the base and perpendicular height were measured if it was triangular or the diameter if it was approximately circular. The surface areas were then calculated using appropriate geometrical formulae. The areas of a random subsample of boulders were also calculated by tracing the boulder shape on plastic sheeting, a method considered more accurate than the use of geometrical formulae. Comparison of the two methods found the geometrical formulae overestimated the area of boulders by 6 percent, on average, but their use was favoured because the tracing of all boulders sampled could not be completed within the time available.

Sediment

Sediment samples were collected after recording the abundances of each chiton species under boulders. At least 30 ml of sediment was collected from under 78 boulders in the low-shore and mid-shore regions. Samples were then dried to constant weight and sieved into 3 fractions. These fractions were fine sand (< 0.425 mm), coarse sand (> 0.425 mm to 1.400 mm) and gravel and shell grit (> 1.400 mm to 3.360 mm). The proportion of each fraction in each sediment sample was determined by weight measured to the nearest 1 mg.

Size of chitons

The size of chitons has been documented by measuring the anterior-posterior lengths of individuals in the field (e.g. Glynn 1970, Baxter and Jones 1978). Such measurements can lead to substantial errors because of the curvature of the substratum (a boulder in this study) underlying any given individual. To avoid this source of error we recorded the width of the fourth shell-plate, or the first shell-plate of *Cryptoplax mystica*, as these measurements are linearly related to the maximum length of the chiton and are not affected by the curvature of the substratum underlying the chiton (Wells and Sellers 1987, Otway 1994 and see Results). The width of the appropriate shell-plate was measured to the nearest 0.1 mm using dial calipers. However, individuals of *Acanthochiton granostriatus* (Pilsbry, 1894) and *A. retrojectus* (Pilsbry, 1894) were not measured because of their small size and because the two species could not be distinguished in the field.

Sampling of chitons

Boulders were overturned and the number of chitons of each species found on the underside of each boulder was recorded. Any chitons that fell from the boulder during overturning were collected, identified and measured before being returned to the base of the boulder when sampling was complete. After sampling, each boulder was returned to its original position and orientation. The densities of all chitons were scaled to the number of individuals 1000 cm^{-2} prior to analysis.

The spatial and temporal patterns in the abundances of under-boulder chitons were documented at four sites: 2 in the mid-shore and 2 in the low-shore regions of the boulder zone. No sampling was done in the high-shore regions because a preliminary survey (Smith 1992) had shown that no chitons were found under boulders in this region. Sampling was done from March to August, 1992. Each month, 20 randomly chosen boulders were sampled from each of 2 replicate areas (3×3 m) randomly located in each of 4 sites (10×10 m). Areas within Sites were at least 3 m apart and Sites at the same height on the shore were separated by approximately 60 m. Each month, new areas were selected at random from within each site to minimize sampling of boulders disturbed by prior sampling. On each occasion, 160 boulders were sampled; 80 from each of the mid- and low-shore regions. It is possible, however, that some boulders were sampled more than once during the 6 months of sampling.

Effects of sampling-induced disturbance

A manipulative field experiment was set up to examine the effects of disturbance on the abundances of under-boulder chitons. We were particularly concerned with changes that may occur following our sampling of the boulders as this could confound our studies of the spatial and temporal patterns of

abundance. The experiment consisted of 3 treatments: an undisturbed control in which the boulders were sampled and then removed from the site, together with any chitons attached to these boulders, to ensure that they were not sampled again (C); a treatment which followed our normal sampling protocol (D) and a treatment in which boulders were sampled and then replaced in an overturned position (O). Boulders in the latter two treatments (D and O) were marked with numbered tags to permit subsequent identification and sampling of the same boulders. During the tagging process, care was taken not to damage or destroy any animals. Those chitons that attempted to crawl away or fell off the rock during tagging were recaptured and placed at the base of the rock when it was returned to the boulder field. The experiment was done during August, 1992 and replicated at 3 sites in the low-shore region. At each site, 18 boulders of similar size were selected at random. Six boulders were then assigned, at random, to each treatment. One month later, the boulders in treatments D and O, plus six undisturbed boulders (selected at random) were again sampled at each site after 1 month to match the sampling interval adopted to document the patterns of abundance.

Analysis of Data

Possible correlations between the densities of chitons and grain size were examined using Pearson's partial correlation analysis. Relationships between the sizes and abundances of chitons and the size of boulders were also examined.

Data concerning the spatial and temporal patterns of under-boulder chitons were analysed using a partially orthogonal, partially nested, four factor analyses of variance with Times – random, Heights – fixed, Areas nested within Heights – random and Sites nested within Months, Heights and Areas – random. Note that this does not permit a test of Heights main effects term, but this is not crucial as the factor Heights was addressed in interaction terms.

The effects of disturbance were assessed by fully orthogonal three factor analyses of variance with Times (Before vs. After) – fixed, Sites – random and Treatments – fixed. To ensure the temporal independence of replicates within each treatment, 3 replicate boulders were chosen at random from the 6 in each treatment at each site to provide the “before disturbance” data. The remaining replicates in the disturbed and overturned treatments provided the “after disturbance” data. Data from 3 boulders (selected at random) from the 6 undisturbed (control) boulders sampled after 1 month (as described in subsection “Effects of sampling-induced disturbance”) also provided “after disturbance” data. This procedure has the potential to reduce the power of the tests for treatment effects. Where possible post-hoc pooling of terms in the original model was done to provide more powerful tests of the remaining sources of variation (see Winer 1971 and Results).

Preliminary tests for homogeneity of variances were done prior to analysis of variance using Cochran's test (Snedecor and Cochran 1980). When necessary, data were transformed following standard procedures (for details see Winer 1971, Underwood 1981a). Post-hoc identification of significant differences among means was done using Student-Newman Keuls (SNK) tests (Winer 1971, Snedecor and Cochran 1980).

Results

Correlations with boulder size

Neither the number of species nor the total number of individuals was correlated with boulder size. The number of individuals of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor*, *Cryptoplax mystica*, *Callistochiton antiquus* and *Ischnochiton smaragdinus* also showed no correlations with boulder size.

The widths of the fourth shell-plate of *I. australis*, *I. elongatus*, *I. versicolor*, *I. smaragdinus* and *C. antiquus* were all linearly related to their anterior-posterior lengths and each regression of length on width accounted for at least 90% of the variation in their lengths (Table 1). The width of the first shell-plate of *C. mystica* was linearly related to the anterior-posterior length and the regression of

Table 1. Regression and correlation analyses for under-boulder chitons at Long Reef. ¹Regressions of the length of the individual on the width first shellplate for *Cryptoplax mystica* and the width of the fourth shell-plate for *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor*, *Callistochiton antiquus* and *Ischnochiton smaragdinus*. ²Correlation coefficients calculated using n=78, partial correlation coefficients calculated using n=75. *, **: significant at $p < 0.05$ and $p < 0.01$ respectively; - : insufficient data.

Species	Maximum shell width	Regression of body length on shell width ¹		Correlation coefficients of boulder size and chiton size in low- and mid-shore regions		Correlation coefficients of chiton abundance and proportion of sediment fractions (partial coefficients given in brackets) ²		
		Regression Equation	r ²	Low-Shore	Mid-Shore	fine	coarse	gravel
<i>I. australis</i>		$y = -2.219 + 2.244x$ (n=70)	0.901	0.328** (n=98)	0.279 (n=22)	0.250* (-0.083)	-0.281* (-0.139)	-0.073
<i>I. elongatus</i>		$y = -0.550 + 3.001x$ (n=68)	0.916	0.071 (n=20)	0.694* (n=12)	0.406** (0.339**)	-0.369** (-0.283*)	-0.279* (-0.277*)
<i>I. versicolor</i>		$y = -0.743 + 2.822x$ (n=16)	0.925	0.863 (n=4)	-	-	-	-
<i>C. mystica</i>		$y = -3.699 + 10.966x$ (n=31)	0.602	0.217 (n=35)	0.089 (n=21)	0.112	-0.104	-0.075
<i>C. antiquus</i>		$y = -2.069 + 2.899x$ (n=41)	0.927	0.118 (n=22)	0.462 (n=9)	0.190	-0.214	-0.054
<i>I. smaragdinus</i>		$y = -1.326 + 2.365x$ (n=18)	0.931	0.381 (n=4)	-	-	-	-

length on width accounted for 60% of the variation in length. Of these, *I. australis* and *I. elongatus* were the largest of the abundant species. In most cases the size of individuals of each species showed no significant correlation with boulder size, however, the sizes of *I. australis* in the low-shore and *I. elongatus* in the mid-shore were positively correlated with boulder size.

Correlations with sediment

Chiton densities were correlated with the proportion of each sediment fraction (Table 1). The abundances of 2 species were significantly related to grain size ($p < 0.05$). The density of *I. elongatus* was positively correlated with the proportion of fine sand ($r = 0.406$), and negatively correlated with the proportions of coarse sand ($r = -0.369$) and gravel ($r = -0.279$). The density of *I. australis* was also positively correlated with the proportion of fine sand ($r = 0.250$) and negatively correlated with the proportion of coarse sand ($r = -0.281$), but not significantly correlated with the proportion of gravel ($r = -0.073$).

The densities of *I. elongatus* and *I. australis* were also significantly positively correlated with each other ($r = 0.449$). Therefore partial correlations were performed to eliminate any effect of one species on the other (Table 1). Eliminating the effect of *I. australis* did not alter the significance of the correlations of *I. elongatus* density with any sediment fraction (fine $r = 0.339$, coarse $r = -0.283$, gravel $r = -0.277$). However, by eliminating the effect of *I. elongatus*, the correlations of *I. australis* density with each sediment fraction were no longer significant (fine $r = -0.083$, coarse $r = -0.139$).

Spatial and temporal patterns of abundance

The number of species and total number of individuals occurring under boulders (Fig. 1) did not exhibit significant temporal variation between Sites nested within Heights on the shore (Table 2,

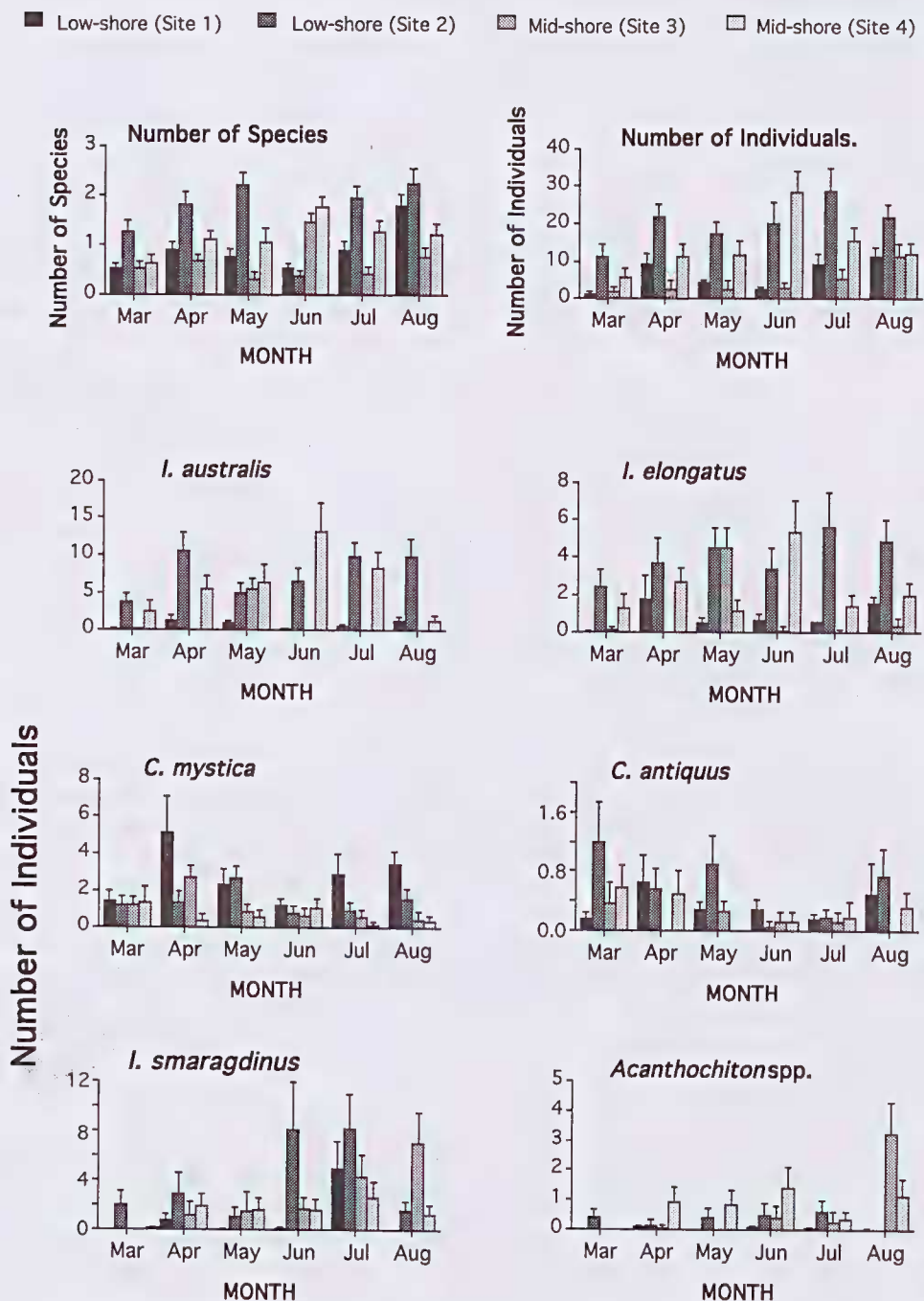


Figure 1. Mean (\pm SE) number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Cryptoplax mystica*, *Callistochiton antiquus*, *Ischnochiton smaragdinus* and *Acanthochiton* spp. found under boulders at replicate sites in the mid- and low-shore regions at Long Reef from March to August, 1993.

Table 2. Analyses of variance of the number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor*, *Cryptoplax mystica*, *Callistochiton antiquus*, *Ischnochiton smaragdinus* and *Acanthochiton* sp. found under boulders in the mid and low-shore regions at Long Reef from March to August, 1993. df: degrees of freedom; MS: mean square; *, ** significant at $p < 0.05$ and $p < 0.01$ respectively; NS: not significant at $p > 0.05$; -: no appropriate mean square denominator for F ratio.

Source of variation	(df)	Number of species		Number of chiton individuals		<i>I. australis</i>		<i>I. elongatus</i>		<i>I. versicolor</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F
Times	5	10.64	*	3.33	NS	0.113	NS	0.092	NS	0.341	NS
Height	1	73.7	-	7.48	-	0.756	-	0.527	-	1.683	-
Sites(Heights)	2	77.85	**	21.35	**	0.554	**	1.052	**	1.941	**
Areas(Sites(Height(Times)))	24	5.63	**	1.35	**	0.127	**	0.068	**	0.136	**
Times x Heights	5	6.4	NS	0.79	NS	0.128	NS	0.078	NS	0.141	NS
Times x Sites(Heights)	10	2.96	NS	1.06	NS	0.092	NS	0.029	NS	0.151	NS
Residual	912	1.08		0.29		0.025		0.020		0.043	
Total	959										

Source of variation	(df)	<i>C. mystica</i>		<i>C. antiquus</i>		<i>I. smaragdinus</i>		<i>Acanthochiton</i>	
		MS	F	MS	F	MS	F	MS	F
Times	5	0.046	NS	0.041	NS	424.85	NS	0.113	NS
Height	1	0.812	-	0.008	-	54.15	-	0.452	-
Sites(Heights)	2	0.087	NS	0.028	NS	511.64	*	0.109	NS
Areas(Sites(Height(Times)))	24	0.065	**	0.008	NS	84.09	NS	0.069	**
Times x Heights	5	0.076	NS	0.011	NS	191.18	NS	0.215	NS
Times x Sites(Heights)	10	0.037	NS	0.016	NS	142.41	NS	0.107	NS
Residual	912	0.018		0.008		74.05		0.036	
Total	959								

analyses of variance, $p > 0.05$). However, both the number of species and total number of chitons differed significantly at the two spatial scales of Sites (60 m apart) and Areas within Sites (3 m apart) (Table 2, analyses of variance, $p < 0.001$). Small-scale differences in the number of species and total number of individuals occurred between Areas in the mid-and low-shore regions (Table 3, SNK tests, $p = 0.05$). At the larger spatial scale, there were significantly more species under boulders at Site 3 in the mid-shore and Site 2 in the low-shore (Table 2, SNK tests, $p = 0.05$). The number of

Table 3. Summary of results of SNK tests showing the months in which abundances of chitons in areas nested within sites were significantly different in the mid- and low-shore regions at Long Reef. (- denotes no significant differences)

Variable	Mid-shore		Low-shore	
	Site 3	Site 4	Site 1	Site 2
Number of species	-	Mar, May, Aug	Apr	Apr
Number of Individuals	-	Mar, May, Jun, Aug	Apr	May
<i>I. australis</i>	-	Mar, Apr, May, Jun, Jul	May	Apr, May
<i>I. elongatus</i>	-	-	-	Mar, Apr, May, Jun, Aug
<i>I. versicolor</i>	-	Aug	-	Apr, Jul
<i>C. mystica</i>	-	Jun	Mar, Apr, Aug	Mar, Apr
<i>Acanthochiton</i> spp.	-	May, Jun, Aug	-	-

individuals only differed between sites in the low-shore with significantly more individuals occurring at Site 2.

The densities of *Ischnochiton australis*, *Ischnochiton elongatus* and *Ischnochiton versicolor* (Fig. 1) did not vary through time at Sites nested within Heights on the shore, but all three species differed at the large and small spatial scales (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). Densities of *I. australis* and *I. versicolor* differed between areas in the mid- and low-shore regions with *I. versicolor* only differing on three occasions (Table 3, SNK tests, $p = 0.05$). However, densities of *I. elongatus* only differed between areas in the low-shore region (Table 3, SNK tests, $p = 0.05$). At the larger spatial scale, *I. australis* and *I. elongatus* had significantly greater densities at Site 2 in the low-shore and at Site 4 in the mid-shore (Table 2, SNK tests, $p = 0.05$). *I. versicolor* on the other hand only differed in the low-shore with significantly greater densities occurring at Site 1 (Table 2, SNK tests, $p = 0.05$).

The densities of *Ischnochiton smaragdinus* and *Callistochiton antiquus* (Fig. 1) did not fluctuate through time at Sites nested within Heights on the shore, but there were significant differences in space (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). Neither *I. smaragdinus* nor *C. antiquus* differed in density between Areas, but both species exhibited significant differences at the larger scale of Sites (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). *I. smaragdinus* had significantly greater densities at Site 2 in the low-shore and did not differ between sites in the mid-shore (Table 2, SNK tests, $p = 0.05$). *C. antiquus* exhibited the opposite pattern and

Table 4. Analyses of variance of the number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor*, and *Ischnochiton smaragdinus* found under boulders before and after experimental disturbance. df: degrees of freedom; MS: mean square; *, **: significant at $p < 0.05$ and $p < 0.01$ respectively; NS: not significant at $p > 0.05$; E: term eliminated from model as $p > 0.25$.

Source of variation	(df)	Number of chiton species		Number of chiton individuals		<i>I. australis</i>	
		MS	F	MS	F	MS	F
Before/After (B/A)	1	14.52	**	312.96	*	112.67	*
Sites(S)	2	3.19	*	333.72	*	88.22	NS
Treatments(T)	2	1.69	NS	304.39	NS	80.72	NS
B/AxS	2	0.07	NS	7.46	NS	4.67	NS
B/AxT	2	9.02	**	324.24	**	77.06	**
SxT	4	3.24	*	95.53	NS	31.03	NS
B/AxSxT	4	0.24	NS,E	4.16	NS,E	3.97	NS,E
Residual	36	0.93		98.89		28.04	
Total	53						

Source of variation	(df)	<i>I. elongatus</i>		<i>I. versicolor</i>		<i>I. smaragdinus</i>	
		MS	F	MS	F	MS	F
Before/After (B/A)	1	5.35	NS	1.53	*	0.07	NS
Sites(S)	2	11.91	NS	0.97	NS	5.06	NS
Treatments(T)	2	21.63	NS	0.92	NS	35.17	NS
B/AxS	2	1.46	NS	0.06	NS	0.35	NS
B/AxT	2	14.52	**	1.79	**	0.91	NS
SxT	4	5.32	NS	1.39	NS	16.06	NS
B/AxSxT	4	0.38	NS,E	0.09	NS,E	1.19	NS,E
Residual	36	10.02		0.58		11.2	
Total	53						

only differed in the mid-shore with significantly greater densities occurring at Site 3 (Table 2, SNK tests, $p = 0.05$).

The densities of *Cryptoplax mystica* and *Acanthochiton* spp. (Fig. 1) did not vary through time at the Sites in the mid- and low-shore regions and only differed significantly at small spatial scales of the Sites (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). *C. mystica* differed between Areas on 6 occasions at the sites in the mid- and low-shore regions (Table 3, SNK tests, $p < 0.05$). The densities of *Acanthochiton* spp. also differed on 3 occasions, but these differences were all confined to Site 4 in the mid-shore (Table 3, SNK tests, $p = 0.05$).

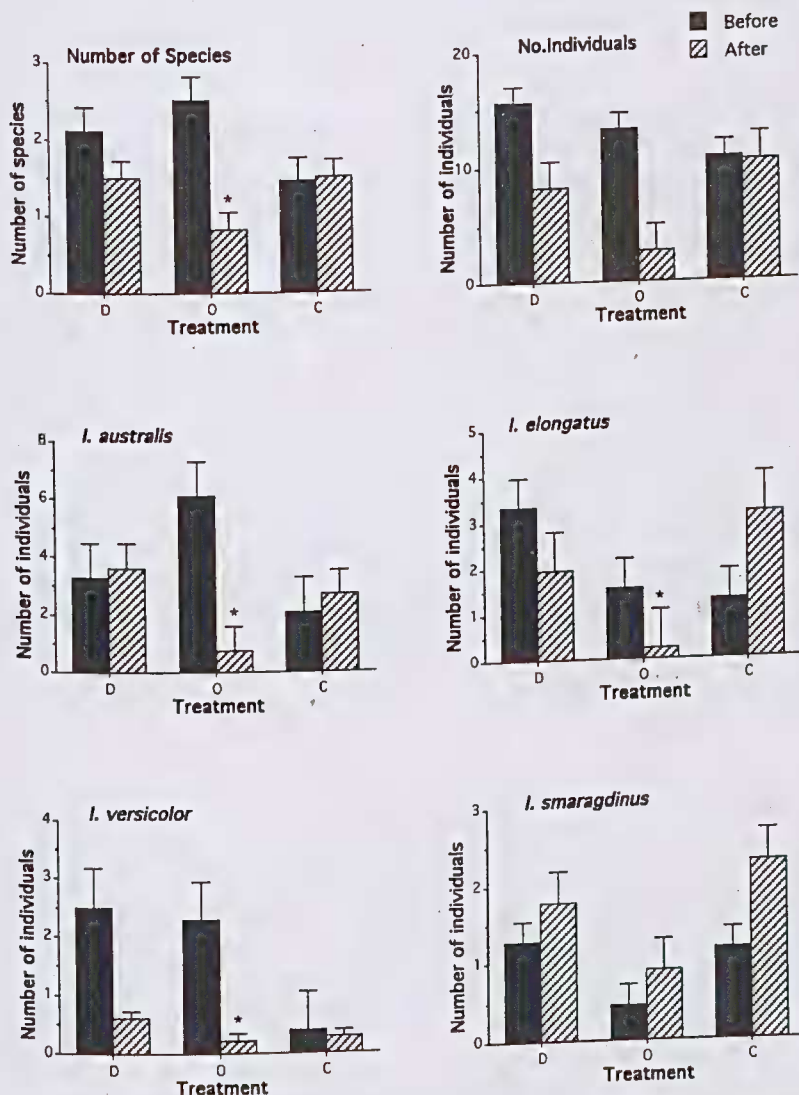


Figure 2. Mean (\pm SE) number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor* and *Ischnochiton smaragdinus* found under boulders disturbed (D), overturned (O) and control (C) boulders at the before and after experimentation. Means of each treatment based on $n=18$ replicate boulders; * $p < 0.05$ from SNK tests.

Effects of Disturbance

The Before/After \times Sites \times Treatments interaction was eliminated from all analyses of variance as the term was not significantly different at $p > 0.25$ (Table 4). This enabled the Before/After \times Treatment interaction to be tested over a new Mean Square Residual and resulted in a test with 2 and 40 degrees of freedom giving substantially more power than the original test with 2 and 4 degrees of freedom (Table 4).

The mean numbers of species (Fig. 2) in each treatment were significantly different from Before to After (Table 4, analysis of variance, $p < 0.01$). Treatments were significantly different prior to disturbance, with the least number of species of chitons under control boulders and the largest under overturned boulders (SNK tests, $p < 0.05$). After disturbance, there were significantly fewer numbers of species found under overturned boulders (SNK tests, $p < 0.05$). The Sites \times Treatment interaction (Table 7) was due to a significantly greater number of species occurring under the disturbed boulders at Site 3 (SNK tests, $p < 0.05$) prior to disturbance. This result was not unexpected as all boulders were initially chosen at random.

The mean number of individuals (Fig. 2) in each treatment were significantly different prior to disturbance (Table 4, analysis of variance and SNK tests, $p < 0.05$). However, after disturbance there were significantly fewer individuals under the overturned boulders (Fig. 2 and SNK tests, $p < 0.05$). There were also significantly fewer individuals under the disturbed compared to the control boulders, but as this was present prior to disturbance there was no effect of our sampling (SNK tests of pooled means, $p < 0.05$).

The effects of disturbance were also evident with individual species, but was restricted to those species with smaller among boulder variation in their abundances. For example, the mean number of *I. australis* in each treatment (Fig. 2) were significantly different prior to disturbance (Table 4, analysis of variance, $p < 0.05$). After disturbance there were significantly fewer *I. australis* under disturbed and overturned boulders, but only those chitons under the overturned boulders differed from before to after (Fig. 2 and SNK tests, $p = 0.05$). The mean number of *I. elongatus* and *I. versicolor* in each treatment (Fig. 2) were not significantly different prior to disturbance, but after there were significantly fewer individuals of both species under overturned boulders (SNK tests, $p = 0.05$). Treatments were not significantly different prior to disturbance, but after there were significantly fewer individuals of both species under disturbed and overturned boulders (SNK tests, $p = 0.05$). However, the abundances of neither species differed from before to after under the disturbed boulders (SNK tests, $p = 0.05$).

Species such as *I. smaragdinus* (Fig. 2 for example), *C. antiquus* and *C. mystica* exhibited large among boulder variation in their abundances and there were few consistent differences present from before to after and among treatments.

Discussion

Our study has documented the spatial and temporal patterns of abundance of 8 species of chiton occurring under boulders at Long Reef. While most of the early studies (Iredale and Hull 1927, Allan 1950, Dakin 1952, Pope 1943) were primarily concerned with describing the chitons and their associated habitats, they did provide some observations that we were able to test. Early studies suggested that the distribution and abundance of some species were influenced by sediment type. We have shown that the abundance of *I. elongatus* increased with the proportion of fine grained sediment. However, the abundances of other species in this study were not related to sediment type. Relationships between sediment-type and the abundance of chitons have been documented elsewhere. For example, the Californian chiton *Stenoplax heathiana* is only found under boulders that are embedded in sand (Ricketts and Calvin 1968, Andrus and Legard 1975). There are also species such as *Ischnochiton maorianus* that are unaffected by the presence of sediment under the boulder (Mortimer 1985).

Relationships between the size of chitons and the size of the boulder are generally unknown although Andrus and Legard (1975) considered the size of *Stenoplax heathiana* to be unaffected by

boulder-size. The sizes of *Ischnochiton australis* and *Ischnochiton elongatus* were positively correlated with the size of the boulder. It is interesting that this correlation with boulder size should occur with *I. australis* and *I. elongatus* as both species are highly sensitive to boulder disturbance. Overturning a boulder elicited the so-called "escape response" with both species immediately curling up and falling off the boulder. Each chiton is then passively transported by water movement until another boulder reached. Other species, such as *C. antiquus* and *I. smaragdinus* displayed a more sluggish response, showing no immediate reaction but eventually moving slowly to the other side of the overturned boulder. These differences in behaviour have also been noted by other workers (e.g. Allan 1950, Ludbrook and Gowlett 1984). It is possible that the correlation between size of the chiton and boulder size is actually determined by the rate of disturbance as McGuinness (1987a) has shown that smaller rocks were overturned more frequently (i.e. \approx once every 2 months) than were larger rocks (i.e. \approx once per year). Thus, due to the disturbance-sensitive behaviour of *I. australis* and *I. elongatus*, larger individuals of these species may accumulate under larger boulders, which are less disturbed.

The height on the shore and size of the boulder has also been thought to affect the abundance of particular *Ischnochiton* species (Dakin 1952), but our study did not support this hypothesis and this result was consistent in the mid- and low-shore regions. In contrast, densities of the New Zealand chitons *Ischnochiton maorianus*, *Amaurochiton glaucus*, *Onithochiton neglectus* and *Rhyssoplax* sp. are, on average, greater under large compared to small boulders (Mortimer 1985).

The abundances of under-boulder chitons showed no significant temporal changes over the six months of this study and any temporal variation that was present was far outweighed by the spatial variation. This result was somewhat unexpected as the abundances of many intertidal organisms along the NSW coast exhibit seasonal changes (O'Gower and Meyer 1965, 1971, Underwood 1981b 1984). It is quite conceivable that marked differences in the abundances of under-boulder chitons may only be evident between the cooler and hotter periods of the year. The under-boulder micro-habitat may only be affected by the extremely low Spring tides occurring during daylight hours in Summer and not by those in Winter when very low tides occur at night. Desiccation during low tides coincident with periods of high temperature is thought to cause substantial mortality for chitons (Glynn 1970, Simpson 1976) and its effects are generally more pronounced higher on the shore (Boyle 1970, Horn 1982). Our study was restricted to the cooler, Autumn and Winter months. Sampling over a further two years and at several (at least 2) heights on the shore would be necessary to determine the combined effects of low tides and high temperatures.

The abundances of the platform-dwelling, intertidal organisms on rocky shores of New South Wales can show considerable variation over a horizontal distance of only a few metres (e.g. Underwood 1981a, Underwood and Jernakoff 1981). This is also true for under-boulder communities (McGuinness 1987a, b). The 8 species of under-boulder chiton also exhibited similar patterns in that their densities differed at two spatial scales: between areas and sites, 3 m and 60 m apart, respectively. This spatial variation was evident in the mid- and low-shore regions. The tendency towards more fluctuations in the mid-shore may be due to a range of stresses associated with increased emersion and desiccation as well as the greater rate of physical disturbance at sites higher on the shore. A combination of these factors is most likely responsible for the general decrease in abundances and lower diversity of chitons under boulders higher on the shore (McGuinness 1987b).

To our knowledge, our manipulative experiment is the first of its kind to examine the effect of sampling-induced disturbance on populations of under-boulder chitons. Overturning of the boulders resulted in significant declines in species-richness, overall abundances and the densities of *Ischnochiton australis*, *Ischnochiton elongatus* and *Ischnochiton versicolor*. The decline in the abundances of chitons on overturned boulders is consistent with the results for boulder communities in general (McGuinness 1987a, b for Long Reef, and elsewhere Osman 1977, Leiberman *et al.* 1979, Sousa 1979).

There is a number of possible reasons why the overturning of boulders caused a decline in the abundances of chitons. Firstly, overturning may simply result in the active or passive movement of

chitons to undisturbed boulders. For some species, the escape response (see earlier) combined with localised water movement may result in passive movement away from the site of disturbance. Dayton *et al.* (1977) observed a similar escape response when the chitons *Chiton cumingsii*, *Chiton granosus* and *Acanthopleura echinata* were approached by the predatory starfish *Meyenaster gelatiosus*. When this occurred the chitons were swept away by the surge and re-attached some distance away from the initial disturbance. Mortimer (1985) has argued that the "escape response" may not enhance survival because remaining on a disturbed boulder may not be detrimental. This was definitely not the case for the predatory interactions described by Dayton *et al.* (1977) as failure to escape was detrimental on almost all occasions.

The overturning of boulders could expose the chitons to predation by visual predators such as birds and fish. While several of the local, rocky-reef fish including *Pagrus auratus*, *Ellerkeldia annulata*, *Ophthalmolepis lineolatus* and *Cheilodactylus fuscus* are known to consume under-boulder chitons (Russell 1971, Bell 1979, Otway unpubl. data, Smith pers. obs.), we do not know whether their foraging is restricted to the subtidal regions or extends into the intertidal regions during high water.

Secondly, the overturning of boulders can reduce the area of substratum available for attachment. The upper surfaces of many boulders in the low-shore are covered by foliose macroalgae, reaching 100% cover on occasions (McGuinness 1987a, Smith 1992). On overturning, the algal-covered lower side has a greatly reduced area available for attachment by chitons, particularly for large individuals of *I. australis*, *I. elongatus* and *I. versicolor*. Small chitons such as *I. smaragdinus*, abundances of which were not affected by overturning, may still find sites for attachment on algal covered boulders.

Finally, the type of micro-habitat found beneath a boulder may also affect distribution and abundance of chitons. For example, rock-type and surface complexity are known to influence the structure of the boulder community at Long Reef (McGuinness 1986). Increased complexity, in the form of pits and grooves, on the under-side of boulders supports more sessile animals, and less complexity resulted in more species of algae. Overturning a boulder can alter the surface complexity by destroying the tubes of polychaetes such as *Diopatra dentata*. Such changes may also affect the chitons as *C. mystica* is frequently found in crevices on boulders, and *Acanthochitona* spp. in small crevices and in between the tubes of polychaetes (Allan 1950, Smith 1992).

Overturning may also alter the micro-habitat in ways that are not readily quantifiable. For example, Pope (1943) noted that *Ischnochiton australis* was frequently found on boulders with a free circulation of water under them. However, the degree of water circulation is difficult to assess quantitatively because sampling may actually impede or alter the water circulation. There are probably many other features of the under-boulder micro-habitat which affect distribution and abundance of chitons. However, to sample the under-boulder community, one must first lift the rock thus altering or destroying the micro-habitat. This is a fundamental problem when working with organisms that occur under boulders.

The manipulative experiment also showed that despite the alterations to the habitat caused by our sampling, the abundances of the under-boulder chitons were not significantly altered indicating that our results were not confounded by sampling-induced disturbance. This result also implies that if sampling is done carefully and boulders are returned as close as possible to their original position and orientation, boulders can be repeatedly sampled with minimal effects on the chiton populations and possibly other organisms. Consequently, we are confident that the abundances documented through time are real and not merely artifacts.

Consideration of sampling-induced disturbance is also relevant to boulder communities in freshwater streams and lakes (e.g. Knott *et al.* 1978, Lamberti and Resh 1979, Bunn 1986). It is clear to us that data concerning spatial and temporal patterns of abundance of macro-invertebrates in boulder communities of freshwater streams will be equivocal if the possible confounding effects of sampling-induced disturbance are not addressed. To avoid such problems, it will be necessary to use manipulative experiments, similar to that used here, to identify the effects of sampling-induced disturbance.

Altogether, our study has documented short-term (over 6 months), spatial and temporal patterns in

the abundances of the 6 main species of chiton that occupy the micro-habitats under boulders. The spatial and temporal patterns documented at Long Reef are only indicative of what may be found in other boulder communities along the New South Wales coast. Future research must ensure that other shores are sampled and the results of such studies will indicate whether the patterns observed at Long Reef can be generalised to similar habitats elsewhere. Furthermore, the spatial variation evident in this study demands that future studies will need to incorporate a range of spatial scales in their sampling designs. Failure to do this will, most likely, disguise patterns associated with different levels of patchiness within these communities. Finally, a greater understanding of the ecology of under-boulder chitons will require demographic studies and the use of manipulative field experiments to identify the proximal causes of patterns in space and time.

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